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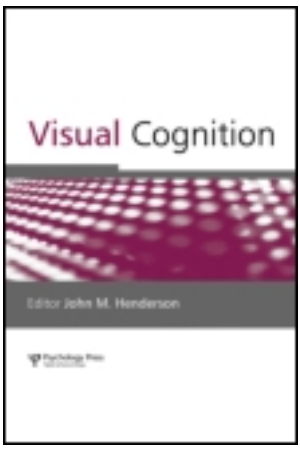


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# Testing the dorsal stream attention hypothesis: Electrophysiological correlates and the effects of ventral stream damage

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The roles of dorsal and ventral processing streams in visual orienting and conscious perception were examined in two experiments. The first employed high density EEG with source localization. The second comprised a neuropsychological case study. Visual orienting was assessed with an attention procedure, where peripheral letters cued participants towards a target location. In the perception procedure participants responded to the same letters by performing an explicit conscious discrimination. In Experiment 1, the peripheral letters elicited rapid dorsal stream activation in the attention procedure, and this activation preceded top-down enhancement of target processing in occipital cortex. In the perception procedure early ventral stream activation was seen. In addition, peripheral letters elicited an "early directing attention negativity" (EDAN) over parietal recording sites in the attention procedure, but not in the perception procedure. In Experiment 2, a patient with a bilateral ventral stream lesion but preserved dorsal stream function showed clear disruption to performance in the perception procedure, whilst exhibiting a

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normal visual orienting effect in the attention procedure. Taken together these findings (1) highlight the distinct roles of the dorsal and ventral streams in attention and perception, and (2) suggest how these streams might interact, via reentrant effects of attention on perceptual processing.

***Keywords:*** Attention; Dorsal stream; Ventral stream; Visual orienting; Visual perception.



When faced with a complex visual scene, our brain somehow has to pick out those items that may be of interest or importance, in order to direct the focus of our selective attention to the best advantage. What visual pathway or pathways are used to achieve this? Cortical visual processing arises from activity in two somewhat distinct neural pathways (Merigan & Maunsell, 1993). The potentially distinct functional specialization of these two streams has, however, been a matter of debate. Mishkin, Ungerleider, and Macko (1983) argued that the ventral pathway, leading from Area V1 in occipital cortex to inferotemporal cortex, was responsible for recognizing what an object is, whereas the dorsal pathway, from V1 to parietal cortex, was responsible for localizing where an object was. Milner and Goodale (1995, 2006) proposed a different interpretation, arguing that "what" and "where" processing was done in both streams but in the dorsal stream the information was used to guide actions, whereas in the ventral stream the information leads to our explicit perception of what and where an object is. Fang and He (2005) provided functional MRI data consistent with Milner and Goodale's proposal that object selectivity is present in the dorsal visual stream. Furthermore Fang and He showed that this dorsal stream object-selective activation was not differentially associated with conscious perception. Only in the ventral stream was the object-selective activation associated with conscious object perception. Thus, there is clear evidence in support of the idea that the contents of conscious visual perception are selectively associated with processing in the ventral stream.

At the same time, however, there is clear evidence that processing in the dorsal stream plays a critical role in influencing what we become conscious of. A case in point is visual extinction following parietal lesions, in which patients do not consciously perceive the more contralesional of two visual stimuli when presented simultaneously. The typical interpretation of this disorder is that it reflects an inability to orient attention towards one side of space. Given the known dissociation between allocating attention and conscious perception (Kentridge, Heywood, & Weiskrantz, 1999), it seems likely that parietal lesions do not influence conscious perception directly, but do so via their role in allocating attention (Milner & Goodale, 1995). We (Lambert & Shin, 2010) have developed a shape-cue contingent spatial priming paradigm that further highlights how perception can be dissociated

from attention. In this paradigm, contingencies between peripherally presented cue items and target location can be rapidly learnt and exploited by the visual system in allocating spatial attention, independently of having consciously perceived the contingent relations between target location and cue items (Shin, Marrett, & Lambert, 2011). Our previous behavioural work has provided some indications that this shape cue-contingent priming effect might be mediated by attentional systems in the dorsal stream (Lambert & Shin, 2010). Here we used high density EEG together with source localization, in combination with a single case neuropsychological study, to test the hypothesis that visual encoding that triggers a shift of attention, in response to a peripheral object, is mediated via the dorsal visual stream. We refer to this later as the dorsal stream attention hypothesis. Furthermore, we use the EEG data to explore how computations performed in both streams could interact via a top-down enhancement of occipital sites from which both streams receive their input.

In our previous paper, we reported an initial test of the dorsal stream attention hypothesis, which exploited known differences in luminance contrast sensitivity between the two visual pathways (Lambert & Shin, 2010). The dorsal stream is composed almost entirely of rapidly conducting fibres originating from magnocellular (M) layers of lateral geniculate nucleus (LGN), and neurophysiological studies have shown that M-cells respond well to low contrast stimuli (Merigan & Maunsell, 1993). In addition, Bullier (2001) has noted the very short response latencies of visually responsive neurons in parietal cortex, and refers to these dorsal stream areas as the "fast brain". The ventral stream, on the other hand, receives input from both parvocellular (P) and magnocellular (M) layers of LGN. P cells exhibit lower contrast sensitivity, and conduct signals more slowly (Merigan & Maunsell, 1993). If attentional orienting in response to peripheral visual stimuli is mediated by encoding in M-system neurons in the dorsal stream, then such effects should be robust even under reduced luminance contrast. Consistent with this, Lambert and Shin (2010) observed a dramatic dissociation between effects of luminance contrast on visual orienting and on conscious perception of peripheral stimuli. In this paradigm, which is essentially an adaptation of the well-known Posner spatial cueing task (Posner, 1980), participants are presented with bilateral spatial cues (e.g., the letters "X" and "T"), and are informed that a target object is likely to appear on the same side as one of the letters (see also Lambert & Duddy, 2002). Participants make a simple detection response to the target, and visual orienting in this situation is indexed by comparing response time on valid trials, where the target appears at the likely location, as indicated by the cue, with response time on invalid trials, where the target appears at the unlikely location. In agreement with the dorsal stream attention hypothesis, Lambert and Shin found that the magnitude of rapid visual orienting effects elicited by

peripheral letter cues was unaffected by the luminance contrast of the cues. This was consistent with two characteristic properties of the dorsal stream—good contrast sensitivity (Merigan & Maunsell, 1993) and rapid signal conduction (Bullier, 2001). Conscious perception of the peripheral letter stimuli was indexed by the speed and accuracy with which participants were able to indicate whether one of the letters (e.g., "X") was on the left or right of the display. It was observed that conscious perception of low contrast peripheral letters was massively slower and less accurate than perception of high contrast peripheral letters. This was consistent both with perceptual phenomenology (the peripheral letters *appeared* faint and difficult to see), and with involvement of slower acting parvocellular (P) pathways, which contribute heavily to the ventral visual stream. Although this finding was in agreement with the dorsal stream attention hypothesis, it nevertheless constitutes somewhat indirect evidence, being based on a pattern of behavioural performance predicted by properties of the dorsal stream—sensitivity to luminance contrast and speed of response. A further caveat is that though robustness under low contrast is certainly a prediction of the dorsal stream attention hypothesis, as we have noted the ventral stream includes neurons fed from both parvocellular *and* magnocellular layers on LGN. Thus, robustness under low contrast could in principle be mediated by the ventral stream, if the task under investigation were performed via the M component of that stream.

Here we tested the dorsal stream attention hypothesis more directly in two experiments. The first examined the electrophysiological correlates of visual encoding of peripheral visual objects, using high density EEG recording, together with source localization. The second tested this dorsal stream attention hypothesis by exploring visual task performance in Patient DF, who has a bilateral lesion to the shape processing area LO in her ventral stream, but preserved dorsal stream function.

## EXPERIMENT 1

Figure 1 illustrates the two tasks used in the experiment. In both tasks, a pair of peripheral letters ("X" and "T") was presented initially, for 67 ms, on the left and right of a visual display. In the attention procedure (upper panel) participants made a speeded keypress response to a target object, having been informed that the target was likely to appear ($p = .75$) on the same side as one of the letters. In this task, the letters acted as figural cues and triggered a shift of spatial attention towards the target location, but participants did not make an explicit response to them. In earlier work we found that participants are able to shift attention very rapidly indeed in this situation. Lambert and Duddy (2002) observed attentional benefits in

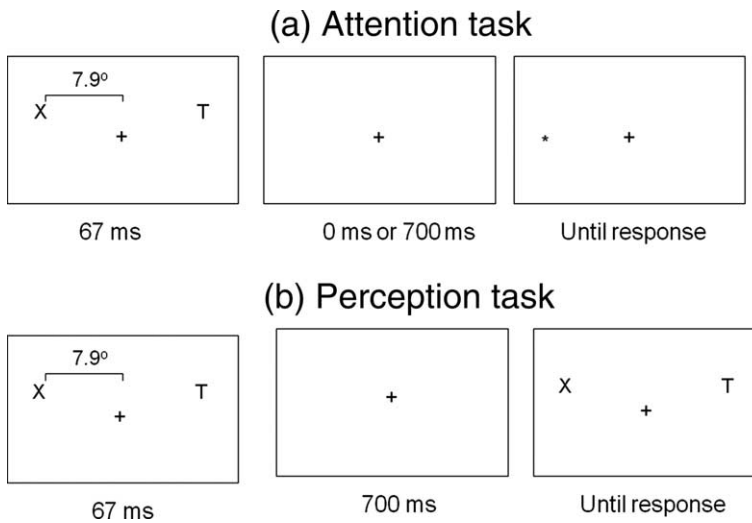


**Figure 1.** Experimental tasks. The upper and lower panels illustrate the sequence of events in each experimental task. In the attention procedure participants responded to the asterisk, and the peripheral letters acted as spatial cues: That is, participants oriented attention towards the likely target location in response to the letters. In the perception procedure, participants made a conscious response to the letters themselves (see main text and Methods for further details).

response to peripheral letter cues, even when there was no delay between onset of the cues and onset of the target. That is, encoding of bilateral letter cues generated immediate top-down facilitation of a simultaneously presented target. In the current experiment the stimulus–onset asynchrony (SOA) between onset of the cues and onset of the target was either zero (cues and targets presented simultaneously) or 700 ms.

In the perception procedure (see Figure 1, lower panel) the initially presented letters acted as a perceptual preview: 700 ms after letter onset the same letters were presented again, and participants indicated with a keypress whether a designated letter was on the left or right of the display. This feature ensured that the temporal structure of the perception procedure was identical with the long (700 ms) SOA condition of the attention procedure, and enabled us to compare directly the neural activation elicited by peripheral letters in the context of the attention and perception procedures, respectively.

The dorsal stream attention hypothesis (Lambert & Shin, 2010), together with findings from our earlier work (Lambert & Duddy, 2002) enabled several predictions to be made regarding performance of these two tasks. These predictions were derived from the proposal of Lambert and Shin (2010) that in the attention procedure "rapid dorsal processing of cue information is followed by re-entrant feedback, leading to ventral stream

facilitation of target processing, manifest behaviourally as the cued trial advantage" (p. 835). Thus, our first prediction was that in the attention procedure the letter cues would generate immediate top-down facilitation of target processing (Lambert & Duddy, 2002). This facilitation should be manifest both behaviourally, in shorter response latencies when the target appears at the cued (valid) location in the zero SOA condition, and electrophysiologically, in enhancement of the P1 event-related potential (ERP) evoked by the target stimulus over occipital recording sites. Previous work, notably by Steven Hillyard's group (Anllo-Vento, Schoenfeld, & Hillyard, 2004) has shown that orienting attention to a visual location is associated with enhancement of the P1 component over occipital cortex, consistent with top-down facilitation of target processing at early sites in the visual pathway. Second, it was predicted that rapid visual orienting, elicited by peripheral letters in the context of the attention procedure would be accompanied by rapid neural activation of the dorsal stream, in response to the cue stimuli. Third, it was predicted that neural activation elicited by peripheral letters in the context of the perception procedure would reveal activation in the ventral stream, and that this activation would have a slower time course than that associated with the dorsal stream (see Bullier, 2001; Lambert & Shin, 2010).

These predictions were tested by using high density EEG, together with a source localization tool, sLORETA (Fuchs, Kastner, Wagner, Hawes, & Ebersole, 2002; Jurcak, Tsuzuki, & Dan, 2007; Pascual-Marqui, 2002). The high temporal resolution offered by this technique allowed us to examine the microtiming of activations in response to cue and target stimuli. Although the spatial resolution of EEG is coarser than that of other techniques such as fMRI, it was sufficient for the purpose of discriminating between activation in the ventral and dorsal streams, which follow anatomically well-separated routes to inferior temporal and superior parietal cortex, respectively.

No previous studies have examined the electrophysiological correlates of visual orienting in response to bilateral peripheral letter cues, as employed in our earlier work (Lambert & Duddy, 2002; Lambert & Shin, 2010). However, several earlier studies have examined the electrophysiological correlates of visual orienting in response to centrally presented arrow-head stimuli (Harter, Miller, Price, LaLonde, & Keyes, 1989; Jongen, Smulders, & van der Heiden, 2007; Nobre, Sebestyen, & Miniussi, 2000; Praamstra & Kourtis, 2010; van Velzen & Eimer, 2003). This work has identified three ERP components elicited by presentation of cue stimuli, each of which is lateralized as a function of whether attention is being directed to the left or right. These components comprise an early directing attention negativity (EDAN), which has been observed between 200 and 400 ms after cue onset, an anterior directing attention negativity (ADAN), which has been observed at frontal and central sites between 300 and 500 ms after cue onset, and a late

directing attention positivity (LDAP), which has been observed at posterior sites at 500–700 ms after cue onset. Because our earlier work has shown that bilateral peripheral cues elicit very rapid visual orienting, leading to the prediction of attentional enhancement even when cues and target are presented simultaneously, it is clear that ERP components with latencies as long as 300–700 ms post cue (ADAN and LDAP) will have little or no functional significance in this task situation. However, it is possible that the earliest component, the EDAN, may be observed in response to peripheral letter cues.

The status of the EDAN has been controversial since van Velzen and Eimer (2003) presented evidence that this component was not related to attention shifting per se, but reflected visual selection of the relevant part of the arrow-head cue stimuli. Visual search studies have shown that visual selection is associated with a negative ERP component, the N2pc, which has a latency similar to the EDAN (Eimer, 1996; Luck & Hillyard, 1994). Van Velzen and Eimer (2003) argued that earlier electrophysiological studies of spatial cueing had misidentified the N2pc, arising from visual selection of the cue stimulus, as a new component, the EDAN. However, in a more recent report Praamstra and Kourtis (2010) have argued that the EDAN and N2pc are indeed separate electrophysiological components. Although the EDAN and N2pc are both negative components with a similar onset latency, these authors present evidence that they have distinct scalp distributions. Although the distribution of the N2pc is known to be posterior and lateral (occipitotemporal), Praamstra and Kourtis showed that the distribution of the EDAN is parietal. This evidence led to a fourth and final prediction regarding performance in the current experiment: That presentation of bilateral letter cues will be associated with an early directing attention negativity (EDAN), observed over parietal electrode sites.

## Method

*Participants.* Thirteen young adults participated in the experiment.

*Procedure.* The procedure used for the attention procedure was similar to that employed previously (Lambert & Duddy, 2002; Lambert & Shin, 2010) and is illustrated in the upper panel of Figure 1. Stimuli were presented in black against a white background, 7.9° to the left or right of a central fixation cross. Visual angles subtended by the letter stimuli were 0.6° (height) × 0.5° (width). The target was a small asterisk subtending 0.5°. Participants responded to a target on the right by pressing the "/" key with their right hand, and responded to a target on the left by pressing the "z" key with their left hand. Half the participants were informed that the target would usually ($p = .75$) appear on the same side as the letter "X"; the other

half were informed that the target would usually appear on the same side as the letter "T". Participants performed 32 practice trials followed by six blocks of 80 experimental trials.

The procedure used for the perception task was similar to that employed previously (Lambert & Holmes, 2004; Lambert & Shin, 2010) and is illustrated in the lower panel of Figure 1. Participants who oriented towards "X" in the attention procedure were required to indicate whether "X" was on the left or right of the display, by pressing the "z" or "/" keys, respectively. Participants who oriented towards "T" in the attention procedure indicated whether "T" was on the left or right. Participants performed 20 practice trials followed by two blocks of 80 experimental trials. The order of performing the attention and perception procedures was counterbalanced across participants.

*EEG recording.* EEG data were collected using 128-channel Ag/AgCl electrode nets (Electrical Geodesics Inc., Eugene, OR) with a sampling rate of 1000 Hz. An average reference was used, and signals were bandpass filtered (0.1–40 Hz) using a digital three-pole Butterworth bidirectional filter. Vertical and horizontal electrooculogram (VEOG and HEOG) were recorded and subsequently employed for artefact rejection

*Statistical analysis.* Analysis of variance was used to compared response times and the amplitude of the P1 evoked potential elicited by the target stimulus in the attention procedure on trials when it appeared at the likely location, as indicated by the letter cues, relative to trials where the target appeared at the unlikely location. These are referred to below as valid and invalid trials respectively. Our sLORETA analyses were performed in two stages. During the first stage, grand averaged ERP data were modelled with sLORETA (see Figure 4a–d). Following this, statistical nonparametric mapping (Manly, 2007; Nichols & Holmes, 2001) was used to compare: (1) Neural activation elicited by the target on valid and invalid trials (see Figure 2c), (2) neural activation elicited by peripheral letters in the context of the perception procedure and in the context of the attention procedure (long SOA condition; see Figure 5a and 5b), and (3) neural activation elicited by peripheral letters that signalled a target on the left and activation elicited by cues for a right target (see Figure 6c and 6d). These analyses were performed using the sLORETA software package (available from http://www.uzh.ch/keyinst/loreta.htm), and were based on techniques described by Nichols and Holmes (2001). Baseline correction and variance smoothing were applied in these analyses.

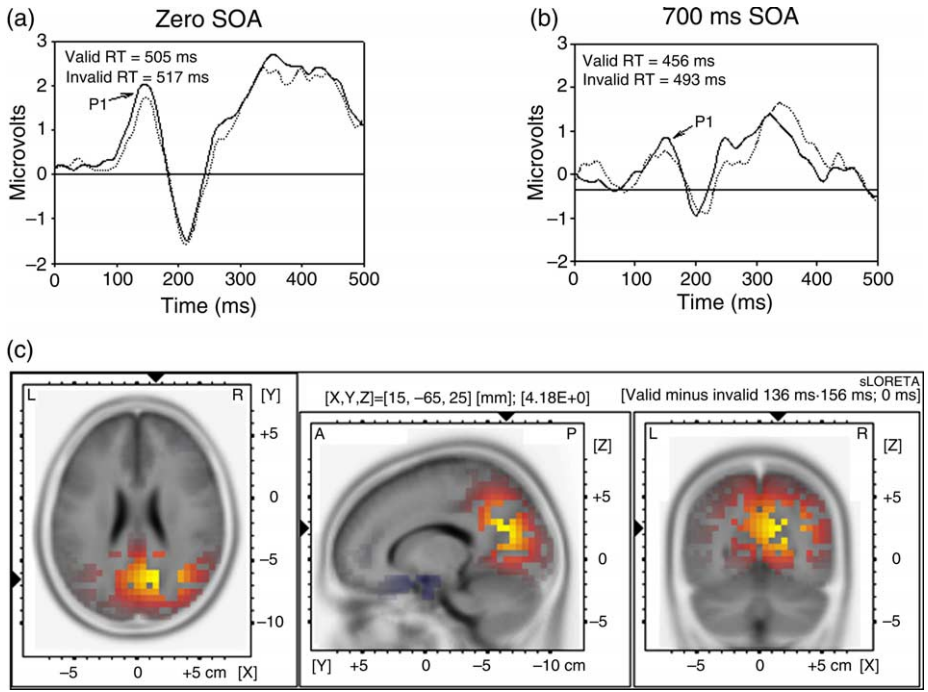


**Figure 2.** Effects of letter cues on target processing. The upper panels (a and b) show that response times were quicker and perceptual processing was enhanced on valid compared to invalid trials. Response times were quicker ($p < .005$) and the P1 evoked potential recorded over occipital electrodes O1 and O2 was enhanced ($p < .02$) on valid compared to invalid trials. Each panel displays the average waveform recorded from electrodes O1 and O2 for valid and invalid trials. The lower panel (c) shows the outcome of statistical nonparametric mapping analysis of the zero SOA condition. Activation on valid and invalid trials was compared within a 20 ms time window (136–156 ms), centred on the P1 peak. Valid trials were associated with stronger occipital activation ($p < .01$), particularly in the precuneus region. To view this figure in colour, please see the online issue of the Journal.

## Results

*Analyses of target processing.* These analyses tested our first prediction, that peripheral letter cues would generate immediate top-down facilitation of target processing. In the analyses, illustrated in Figure 2, electrophysiological activity evoked by the target stimulus, and response times to the target were compared between valid trials, where the target appeared at the likely location, as indicated by the letters, and invalid trials, where the target appeared at the less likely location. It was especially important to establish the presence of a reliable difference between valid and invalid trials in the zero SOA condition in these analyses, because this condition bears directly upon our prediction that peripheral letter cues will elicit immediate top-down facilitation of target processing. Although several earlier studies have examined the electrophysiological consequences of spatial cueing on target processing, most of these studies have used centrally presented cues, and those studies that have employed peripheral cues (Anllo-Vento, 1995; Doallo et al., 2004; He, Humphreys, Fan, Chen, & Han, 2008; Hopfinger & Mangun, 2001) have all employed longer cue–target SOAs. Because this is the first study to examine the electrophysiological sequelae of presenting bilateral peripheral cues with a zero SOA condition, it was important to discover whether the behavioural effects documented in our earlier work (Lambert & Duddy, 2002) would be accompanied by electrophysiological effects that resemble those reported in other studies of spatial cueing (Anllo-Vento et al., 2004; Klein, 2004).

Response times were faster on valid compared to invalid trials, $F(1, 12) = 15.45$, $p < .005$ (see Figure 2a,b). Although this effect varied as a function of cue–target SOA, $F(1, 12) = 9.36$, $p < .02$, the valid trial advantage remained reliable when data from the zero SOA condition were examined separately, $t(12) = 2.74$, $p < .02$. Valid trials were also associated with an enhancement of the P1 component of the target evoked potential, recorded over occipital electrodes O1 and O2 (see Figure 2a,b), $F(1, 12) = 8.19$, $p < .02$. This effect did not vary as a function of cue–target SOA, target visual field, or electrode site (O1 vs. O2). In earlier studies, both these effects have been linked with focusing covert attention on a target location (Anllo-Vento et al., 2004; Klein, 2004).

Response times were quicker overall in the 700 ms SOA condition (475 ms), compared to the zero SOA condition (511 ms), $F(1, 12) = 32.58$, $p < .001$. In keeping with earlier studies of spatial cueing (e.g., Lambert & Hockey, 1986), we interpret this as reflecting a general warning signal effect (Niemi & Naataanen, 1981). That is, presentation of the cue provides a general warning that a target is about to be presented, in addition to providing spatially specific information about where the target is likely to appear.

We then used sLORETA together with statistical, nonparametric mapping (SnPM) (Manly, 2007; Nichols & Holmes, 2001) to compare neural activation on valid and invalid trials in the zero SOA condition. The results, illustrated in Figure 2c, confirmed that the P1 enhancement effect shown in Figure 2a was accompanied by stronger activity in the occipital lobe. Activation on valid and invalid trials was compared within a 20 ms time window (136–156 ms), centred on the P1 peak. Valid trials were associated with stronger occipital activation, $t(12) = 4.18$, $p < .01$, particularly in the precuneus region. Thus, our first prediction was confirmed. Peripheral letter cues produced immediate, top-down attentional enhancement of a simultaneously presented target, and this enhancement was apparent in both behavioural and electrophysiological measures. An important corollary of this finding is that the time course of the cue encoding processes responsible for generating this attentional enhancement must be very rapid indeed (see later).

*Analyses of letter processing in the attention and perception procedures.* Participants' mean response time to the bilateral letters in the perception procedure was 379 ms. Our second and third predictions were tested by examining electrophysiological activations evoked by the peripheral letter stimuli. These analyses focused on the long SOA condition of the attention procedure, and on comparisons of this condition with the perception procedure. In both these conditions peripheral letters were presented on their own, 700 ms prior to a display that required a response.

Figure 3 shows waveforms recorded from occipital electrodes (O1 and O2) and occipitoparietal electrodes (PO7 and PO8) in response to peripheral letters in the long SOA condition of the attention procedure and in the perception procedure. In addition, this figure shows waveforms recorded from parietal (P3 and P4), central (C3 and C4) temporal (T3 and T4), and posterior midline (Pz and POz) electrodes in the two tasks. As this figure shows, the early morphology of waveforms observed in the two task contexts is closely similar. The earliest identifiable feature is a positive going component in the occipital waveforms, the P1, which commences at around 80 ms and reaches a peak at about 145 ms in both the attention procedure and the perception procedure (see Figure 3, upper two panels). Our analyses of the zero SOA condition of the attention procedure (see earlier) had shown that top-down enhancement of target processing was apparent within 136–156 ms of cue onset. Therefore the cue encoding processes responsible for generating this attentional enhancement must have occurred even earlier. This consideration led us to depart from the normal practice of applying source analysis to the peak of an ERP component under consideration, the P1 in this case, because its latency was clearly subsequent to the process of

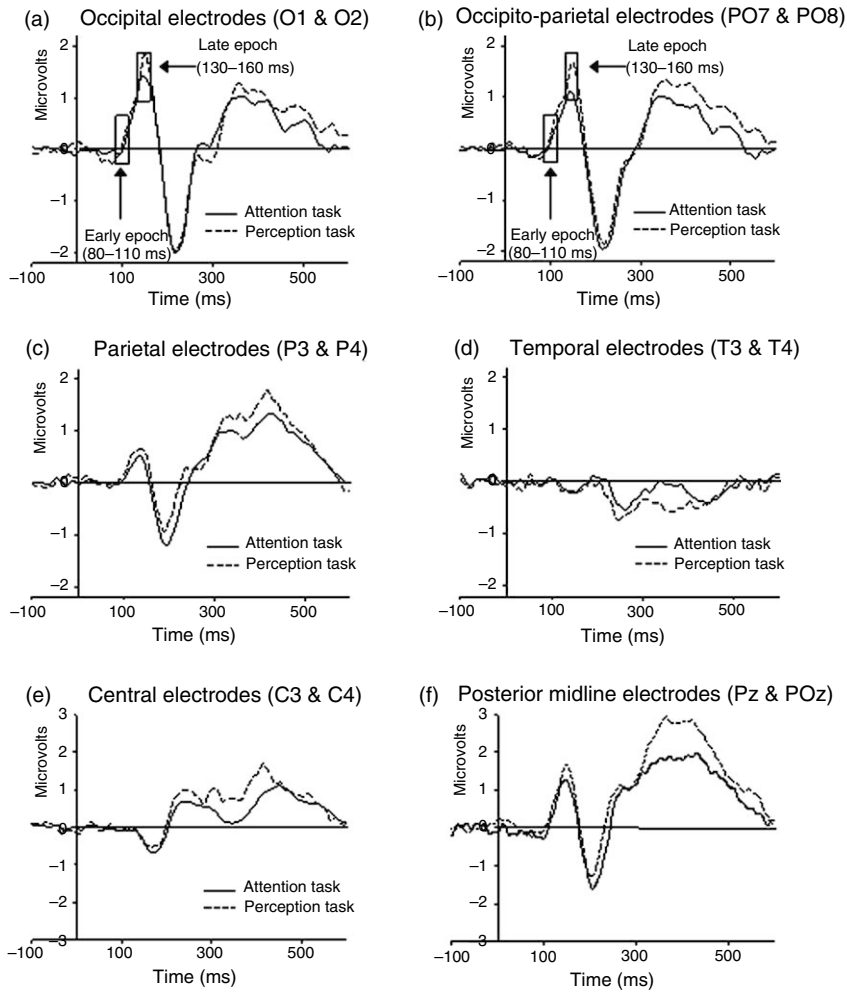


**Figure 3.** Occipital, temporal, parietal, central, and posterior midline waveforms in response to letter cues in the attention and perception procedures. The average responses recorded from occipital (O1 and O2; panel a), occipitoparietal (PO7 and PO8; panel b), parietal (P3 and P4; panel c), temporal (T3 and T4; panel d), central (C3 and C4; panel e), and posterior midline (Pz and POz; panel f) electrodes, in response to peripheral letters presented in the context of the attention procedure (SOA 700 ms condition) and the perception procedure are shown.

interest—the cue encoding processes that generated immediate enhancement of target processing in the zero SOA condition. Therefore, source analysis was applied to an earlier epoch (80–110 ms), which corresponded to the onset of the earliest positive going component of the waveforms illustrated in Figure 3a,b.

The upper panels of Figure 4 show average scalp topographies, together with the outcome of sLORETA analyses applied to the attention and perception procedures during this early time window (80–110 ms from letter onset), corresponding to the onset of the P1 depicted in Figure 3). The lower panels of Figure 4 show average scalp topographies and the outcome of sLORETA analyses during a later time window (130–160 ms from letter onset), which was centred on the peak of the P1 shown in Figure 3a,b. When the letters served as spatial cues in the attention procedure, early activation was apparent in the dorsal pathway, particularly in the right hemisphere (see Figure 4a). The sLORETA solution suggested maximal activation in the superior parietal lobule of the right hemisphere. Thus, our second prediction, that letter encoding in the context of the attention procedure, would elicit rapid dorsal stream activation was confirmed. In contrast, when the letters served as perceptual previews, in the perception procedure, sLORETA indicated early activation at a high level of the ventral pathway, in the inferior temporal gyrus (ITG; see Figure 4b). In the later epoch, corresponding with the peak of the P1 component of the potential evoked by the letter stimuli, sLORETA analysis indicated very similar patterns of activation in the attention and perception procedures. In both cases this was characterized by widespread occipital activation (see Figure 4c, 4d). It is notable that closely similar patterns of occipital activation observed at the peak of the P1 waveform in each task, had dramatically different precursors, involving high level dorsal and high level ventral activation in the attention and perception procedure*s* respectively.

Statistical nonparametric mapping was used to compare early activation elicited by letters in the context of the attention procedure with activation elicited by the same stimuli in the context of the perception procedure. Consistent with the visual impression gained from comparing Figure 4a with Figure 4b, this confirmed that early activation patterns elicited by peripheral letters in the two task contexts differed reliably. As Figure 5 shows, this difference had two principal sources. First, letters elicited stronger early activation in the superior parietal lobule of the right hemisphere when they acted as spatial cues in the attention procedure, $t(12) = 2.25$, $p < .05$. The orange coloured voxels shown in Figure 5a indicate sites with greater activation in the attention procedure, compared to perception procedure. Second, letters elicited stronger early activation in the fusiform gyrus of the left hemisphere when they served as perceptual previews in the perception procedure, $t(12) = 2.73$, $p < .02$ (see Figure 5b). The blue coloured voxels shown in Figure 5b indicate sites with greater activation in the perception procedure compared to the attention procedure.

*Analyses of lateralized ERP components elicited by letter cues in the attention procedure.* Our fourth prediction was that an early directing

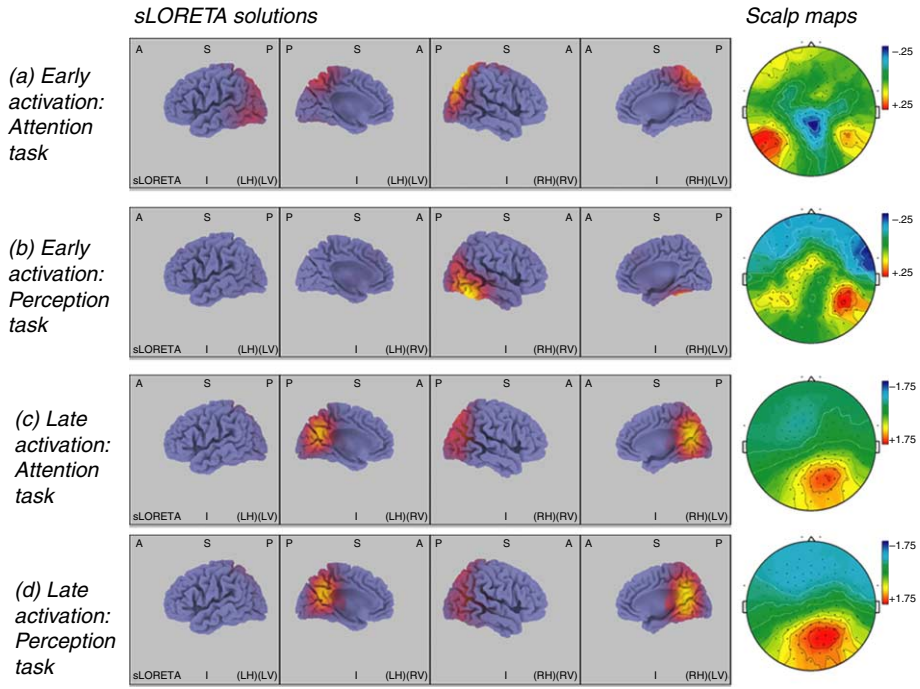


**Figure 4.** Neural activation in the attention and perception procedures. sLORETA revealed a striking dissociation between the cortical sources of early activation evoked by peripheral letters in the two experimental tasks. During the early epoch (80–110 ms after letter onset) activity in the attention procedure was observed at sites corresponding to the dorsal visual pathway, with maximal activation in the superior parietal lobule (SPL; panel a). During the same epoch, activity in the perception procedure was observed at sites corresponding to the ventral pathway, with maximal activation in the inferior temporal gyrus (ITG; panel b). During the later epoch (130–160 ms after letter onset) evoked activity in the two task contexts appeared indistinguishable, and was characterized by widespread occipital activity, particularly in the precuneus region (panels c and d). The rightmost frame of each panel shows the average scalp topography for the early (panels a and b) and late (panels c and d) temporal epochs in each task context. To view this figure in colour, please see the online issue of the Journal.

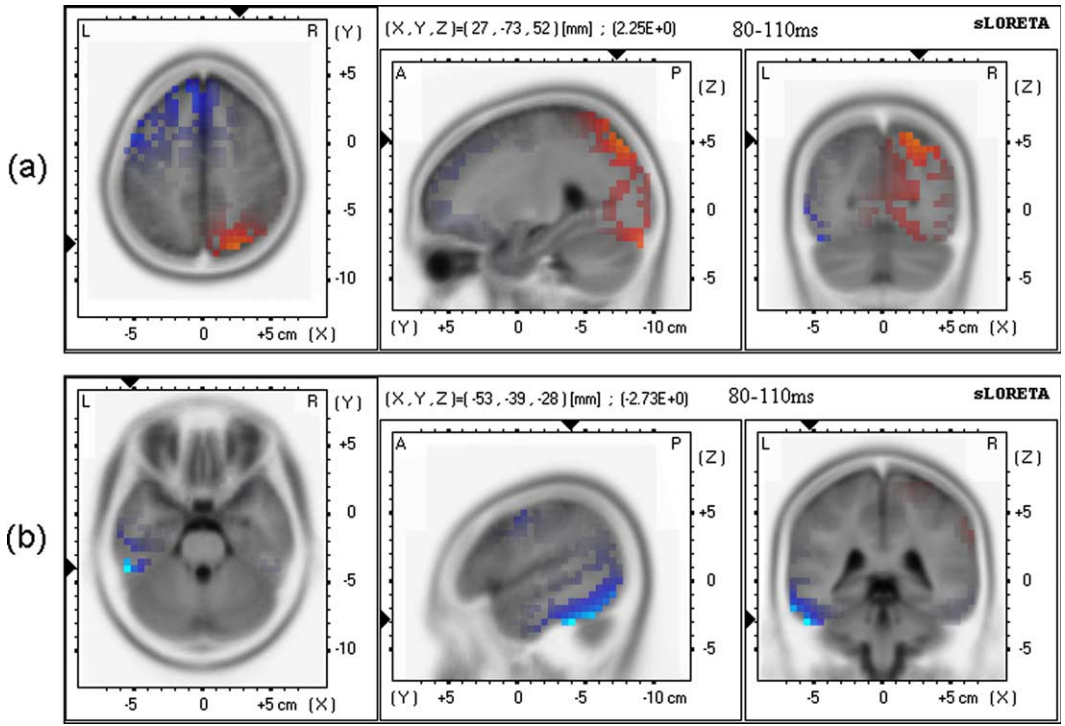


**Figure 5.** Comparison of early activation in the attention and perception procedures. Early activation evoked by letters in the context of the two experimental tasks was compared. Orange coloured voxels indicate sites with greater activation in the attention procedure, compared to perception procedure; blue voxels indicate sites with greater activation in the perception procedure. Panel a shows that stronger activation was observed in the attention procedure at parietal and superior parietal sites ($p < .05$). Panel b shows that stronger activation was observed in the perception procedure at sites in the inferior temporal lobe ($p < .02$). To view this figure in colour, please see the online issue of the Journal.

attention negativity (EDAN) would be observed between 200 and 400 ms after cue onset at parietal electrode sites (Jongen et al., 2007; Praamstra & Kourtis, 2010). This prediction was tested by comparing ERP waveforms at parietal electrodes elicited by cues indicating contralateral and ipsilateral targets. Figure 6a shows the ERP waveforms elicited by these contracues and ipsicues,[1] plotted separately for a group of four left parietal electrodes (electrodes 42, 47, 52 [P3], and 54), and a homologous group of right parietal electrodes (electrodes 86, 92 [P4], 93, and 98; see Praamstra & Kourtis, 2010). The presence of an EDAN is shown in this figure by greater negativity in the ERP waveforms for contracues. A tendency of this kind is first apparent at both left parietal and right parietal electrode sites from about 225 ms to 275 ms post cue onset (see Figure 6a). To explore the scalp topography of this effect, the average response from 225 to 275ms post cue onset to cues indicating a right target was subtracted from the average response to cues indicating a left target during the same period. This left cue – right cue subtraction returns positive values over the left hemisphere (greater negativity in response to right cues) and negative values over the right hemisphere (greater negativity in response to left cues), in the presence of an attention-related negativity. Figure 6b shows the scalp topography of this difference signal. Consistent with the presence of an EDAN, the left hemisphere displays a region where the subtraction returned positive values, whereas the right hemisphere shows a negative region. Although both regions include parietal recording sites in agreement with prediction, some asymmetry is apparent in the distribution. The positive region over the left hemisphere appeared to have a parietal-central distribution, while the negative region over the right hemisphere appeared to have a parietal-temporal distribution. To establish the statistical reliability of the attention related negativities apparent over different cortical regions, three further analyses were undertaken, each of which employed the double subtraction technique used by Kiss, van Velzen, and Eimer (2008). In this technique the difference between the left and right cue conditions for a set of left hemisphere electrodes is subtracted from the difference between the left cue and right cue conditions for homologous electrodes over the right hemisphere. This double subtraction quantifies the degree of attention related negativity across both hemispheres. A one-sample *t*-test can then be used to evaluate the double subtraction values against the null hypothesis of no difference between left and right cue conditions over left and right hemisphere recording sites. This procedure was followed for the parietal group of electrodes listed earlier, for a group of central electrodes

[1] It is important to remember here that the cue stimuli themselves were always bilateral. Contracues and ipsicues were cues that indicated a contralateral and ipsilateral target, respectively.

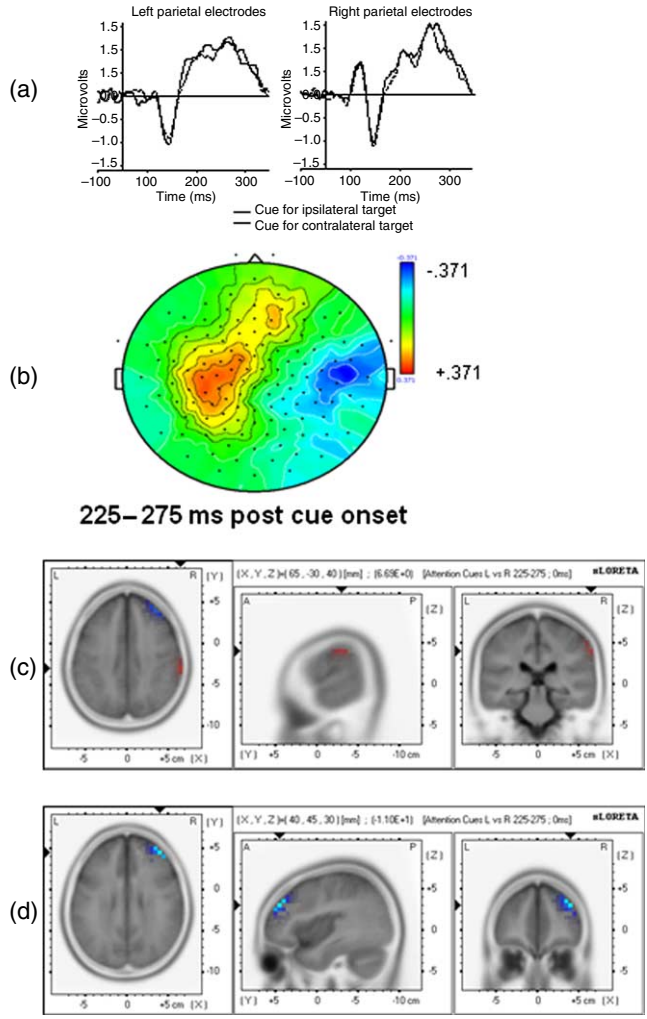


**Figure 6.** Early directing attention negativity (EDAN) in response to cue letters. Panel a shows the average waveforms at four left parietal and four right parietal electrodes (see main text for further details of each electrode group) that were elicited in response to cue letters indicating ipsilateral and contralateral targets. A statistically reliable EDAN was observed 225–275 ms post cue onset (see Results). Panel b shows the average scalp topography recorded during this temporal epoch. Panel c shows the parietal area of the right hemisphere (inferior parietal lobule) that was identified by statistical nonparametric mapping (see Results) as being more active in response to the cue for a left target. Panel d shows the right frontal area (middle frontal gyrus) that was identified by statistical nonparametric mapping as being less active in response to the cue for a left target (i.e., more active in response to the cue for a right target; see Results). To view this figure in colour, please see the online issue of the Journal.

(left hemisphere electrodes: 29, 30, 36 [C3], 37; right hemisphere electrodes: 87, 104 [C4], 105, 111) and for a group of temporal electrodes (left hemisphere electrodes: 40, 41, 45 [T3], 46; right hemisphere electrodes: 102, 103, 108 [T4], 109). These analyses suggested that enhanced negativity contralateral to the direction of cued attention was reliably present over parietal, $t(12) = 2.43$, $p < .05$, and central, $t(12) = 2.67$, $p = .02$, electrode sites, but not over temporal sites, $t(12) = 1.84$, *ns*.

In addition, statistical nonparametric mapping and sLORETA was used to compare activation elicited by letter cues that signalled a left target, with activation elicited by letter cues signalling a right target, during the epoch that spanned 225–275 ms post cue onset. Consistent with the analyses described in the previous paragraph, this contrast highlighted a right parietal area (inferior parietal lobule), that exhibited stronger activity following cues that signalled a contralateral (i.e., left) target, $t(12) = 6.69$, $p < .01$ (see Figure 6c). However, there was no reliable evidence of increased, or reduced, activity in any left hemisphere regions, following a cue that signalled a right (contralateral) target. The contrast between left cues and right cues revealed a further right hemisphere area, characterized by *reduced* activity following a cue for a left (contralateral) target (i.e., relatively stronger activity following a cue for a right (ipsilateral) target), $t(12) = 11.0$, $p < .01$. This region was located in the middle frontal gyrus (see Figure 6d).

A directly analogous set of analyses was then performed to test for the presence of a lateralized negative component in response to bilateral letters presented (as perceptual previews) in the context of the perception procedure. In this case, lateralization was assessed with respect to whether a target letter appeared on the left or right of the display. No lateralized negativity was apparent in the perception procedure for any of the three electrode groups ($t < 1$ in all cases).

Visual inspection of Figure 6a suggests the presence of a second phase of attention related negativity beginning at about 325 ms and ending at about 375 ms post cue onset. However, this tendency was not reliable statistically for any of the three electrode groups.

## Discussion

Results from Experiment 1 speak to two main issues. First, the results provide direct support for the dorsal stream hypothesis—that the visual processing that triggers an attention movement relies on dorsal stream encoding. This hypothesis predicts that dorsal stream structures should be activated when participants encode peripheral objects that serve as cues for an attention movement. The activations illustrated in Figure 4a and 5a show

that this prediction was confirmed.[2] Second, the results show that the electrophysiological correlates of bilateral letter cues resemble those described in earlier studies of spatial cueing (see Anllo-Vento et al., 2004).

*Relation of the current study with earlier work on spatial cueing of attention.* Although the behavioural effects of presenting bilateral letter cues to participants in a spatial attention procedure are now well documented (Lambert, 2003; Lambert & Duddy, 2002; Lambert & Holmes, 2004; Lambert, Norris, Naikar, & Aitken, 2000; Lambert, Roser, Wells, & Heffer, 2006; Lambert & Shin, 2010; Shin et al., 2011) this is the first study to probe the electrophysiological sequelae of bilateral peripheral cues. Results from the experiment show that in two important respects, the electrophysiological correlates of bilateral peripheral cues show close correspondence with effects reported in earlier studies of spatial cueing using both central and peripherally presented cues (Anllo-Vento et al., 2004; Doallo et al., 2004; He et al., 2008; Praamstra & Kourtis, 2010). First, bilateral cues generated an enhancement of the P1 component of the ERP elicited by the target stimulus. Interestingly, this effect occurred even when there was no delay between onset of the cue letters and onset of the target stimulus, indicating that the time course of the cue encoding that generated this attentional enhancement was extremely rapid. Indeed, this time course appears to be more rapid than that observed in studies that have employed centrally presented arrows as cues—even though the latter are presented in high acuity central vision, rather than peripherally. One would expect that cue discrimination would be performed more rapidly in central vision than in parafoveal or peripheral vision. At first sight, this might seem paradoxical, but as we have argued elsewhere (Lambert & Duddy, 2002; Lambert et al., 2006; Shin et al., 2011), the critical factor determining the speed and strength of visual orienting effects in spatial cueing studies of attention is not the visual location of the cue stimuli (central vs. peripheral), nor the requirement to discriminate between cue stimuli (peripheral changes or onsets vs. discrimination of left–right arrows), but the presence of *spatial correspondence* between a cue stimulus and a target object. The current experiment embodied this feature because the location of the target asterisk usually corresponded with the location of one of the peripheral letter cues (Lambert

[2] Although the activations illustrated in Figures 5a and 6a confirm the prediction of the dorsal stream attention hypothesis, it is possible that activity in the tectopulvinar visual pathway could also have contributed to activation of these structures. With EEG techniques of the kind used here it is not possible to evaluate the relative contribution of the dorsal cortical visual pathway and the tectopulvinar pathway to the parietal activations illustrated in Figures 5a and 6a. However, evidence from an fMRI study that is currently underway is likely to shed light on this issue.

et al., 2006). Therefore, in light of our earlier work, rapid orienting was expected, and was observed, both behaviourally and electrophysiologically: In the zero SOA condition, response times were quicker on valid than invalid trials, and an enhancement of the P1 component of the target ERP was observed on valid trials.

A second correspondence with earlier studies of spatial cueing is that the ERP waveform observed in response to the cue letters included an EDAN (early directing attention negativity) component. As indicated earlier, the status of the EDAN and whether it is distinct from the N2pc component has been a topic of some controversy (Praamstra & Kourtis, 2010; van Velzen & Eimer, 2003). The current results provide support for the contention of Praamstra and Kourtis (2010) that the EDAN and N2pc are indeed separate components. Consistent with data reported by Praamstra and Kourtis, a statistically reliable EDAN was observed over parietal and central recording sites which are clearly distinct from the lateral occipital sites associated with the N2pc (see Praamstra & Kourtis, 2010, for analysis of N2pc scalp topography). Furthermore the N2pc has been observed in studies, where participants make an explicit perceptual response to a target object that is selected and discriminated from one or more nontargets (Eimer, 1996). If the N2pc and the EDAN are indeed one and the same component, one would expect that this component would also be observed in the perception procedure, because in this task participants must select and respond to one of the peripheral letters while ignoring the other. Our observation that an EDAN was observed in response to letters in the attention procedure, but not in the perception procedure supports the view that a central-parietal EDAN, associated with movements of attention is distinct from the lateral-occipital N2pc, associated with selecting and responding explicitly to objects in multielement displays.

On the other hand, our EDAN findings contrast with results reported by McDonald and Green (2008), who also used sLORETA to estimate the source of activity evoked by a spatial cue. In this study, sLORETA indicated that the source of activity 250–300 ms post cue onset, evoked by centrally presented cues comprising a colour change, was in occipital cortex. The most salient difference between the McDonald and Green (2008) study and the present experiment appears to lie with the nature of the cue stimuli. In McDonald and Green these comprised a change in the colour of lateralized boxes, that were present on the display at relatively central locations from the beginning of the trial; in the current study the cues were peripheral onset stimuli—the bilateral letters. At this stage, it is unclear which of these candidate factors—central versus peripheral cue location, onset versus no onset cues; colour encoding versus shape/letter encoding—is responsible for the contrast between our findings and those of McDonald and Green.

Although the EDAN observed in the present study was correlated with whether participants oriented attention to left or right, the functional significance of this ERP component with respect to attention shifting is unclear. It is clear from our analysis of performance in the zero SOA condition of the attention procedure that movements of covert attention in this setting were achieved rapidly, with a latency well below the quarter of a second or so which elapsed between cue onset and the EDAN (see Figure 6). Thus it appears that the EDAN, though correlated with the orientation of attention, is not reflecting directly the critical cue encoding process that generated covert orienting in this setting. A similar point applies a fortiori to components with even longer latencies, the ADAN and LDAP, which have been observed in some spatial cueing studies (Jongen et al., 2007).



## EXPERIMENT 2

The results of Experiment 1 are consistent with the central prediction that EEG activity during the attention procedure would be primarily associated with a rapidly emerging signal in the dorsal stream, whereas the perception procedure would be associated with signals in the ventral stream. Experiment 2 seeks to test the causal implications of these EEG correlates by exploring performance on these tasks in a patient (DF) who has a bilateral lesion to her ventral stream that severely impairs form perception. If the differences seen in the dorsal and ventral streams in Experiment 1 truly reflect the differential *causal* involvement of these streams in each of these tasks, then one should expect the perception procedure but not the attention procedure to be disrupted in this patient. Indeed given this patient's profound visual form agnosia, her perceptual performance is highly likely to be disrupted. The critical question therefore is whether her preserved dorsal stream function will be sufficient to generate the shape contingent cueing effect in the attention procedure, despite a predicted poor performance on the perception task.

### Method

*Participants.* DF was aged 56 at the time of testing. Her clinical background has been described in detail elsewhere (Milner & Goodale, 2006; Milner et al., 1991) including combined anatomical and functional MRI scans of her brain by James, Culham, Humphrey, Milner, and Goodale (2003). DF has severe difficulties in discriminating simple geometric shapes (so-called "visual form agnosia"), including individual alphanumeric stimuli. This perceptual deficit is directly attributable to her bilateral lesion of area

LO, the ventral stream area responsible for basic form perception (James et al., 2003; Malach et al., 1995).

In addition, four control healthy control participants were recruited from the Leuven Experimental Psychology department (two female, mean age 23).

*Procedure.* All experimental procedures were identical to the behavioural tasks used in Experiment 1, except for the details listed here. The target was a square subtending 2° degrees of visual angle, and targets and letters (height 1.3°, width 1.2°) were presented at 9° degrees either side of fixation. The SOA between cue onset and target onset was always 150 ms. The background of the display was black. Participants responded with the "W" key to targets on the left and the "N" key to targets on the right. DF completed two 10-trial blocks as practice runs, then two 40-trial, and then sixteen 80-trial experimental blocks of the attention procedure with the "T" as the prime. All four control participants completed a practice block followed by 20 blocks of 80 trials; two of the control participants were primed using the "T" and two with the "X". The prime was valid on 80% of trials. The perception procedure was adapted such that participants were presented with an "X" and a T9° either side of fixation for 67 ms. Participants had to indentify on which side a particular letter was presented. DF and all control participants completed one block of this perception procedure after the attention procedure.

*Results analysis.* All results are based on accurate responses longer than 100 ms, but within 1000 ms of the target onset. Mean response times are calculated only for correct responses. Statistical comparisons between the performance of Patient DF and the performance of controls were carried out using specifically designed tools by Crawford and Garthwaite (2002, 2007) to analyse single case studies in comparison to small control samples.

## Results

A *t*-test on the reaction times to valid vs invalid trials revealed a significant cueing effect for DF and all four control participants (see Figure 7) in the attention procedure. Indeed most critically the cueing effect manifest in DF's reaction times does not differ from that seen in controls ($p = .87$).

DF's performance in the perceptual procedure was however significantly disrupted, in that she correctly identified the side on which a letter was presented on only 66% of trials (chance 50%) compared to a mean accuracy of 95.6% for controls. This difference in accuracy on the perceptual task was highly significant ($p < .001$). It should be noted that DF was adamant that she could not see any letters during the attention procedure, let alone discriminate on which side of the screen there was an "X" or a "T". She was

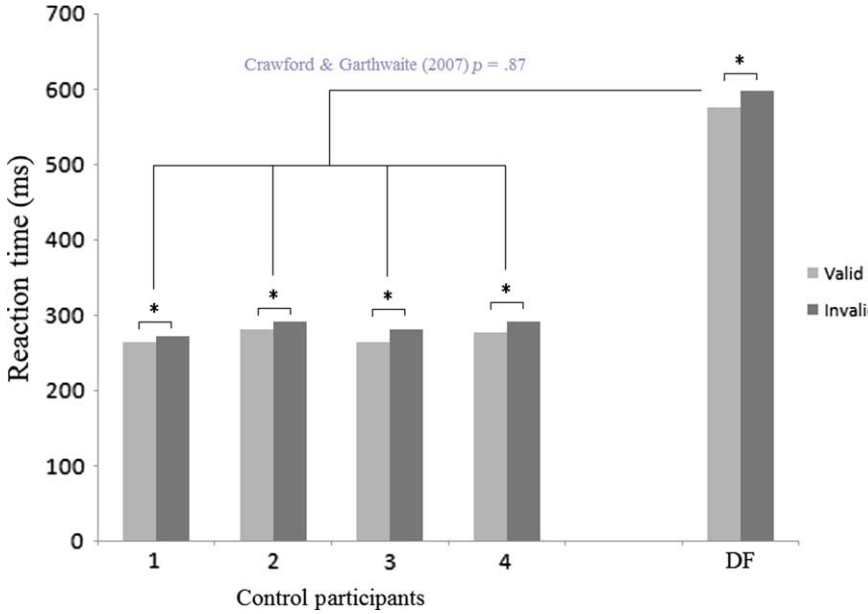


**Figure 7.** Reaction times to valid and invalidly cued targets for Patient DF and four control subjects. The asterisks indicate a significant *t*-test ($p < .05$) comparing the individual reaction times for valid and invalid trials for each participant. DF and every control participant showed a significant cueing effect. Furthermore, using Crawford and Garthwaite's (2007) statistic we found that the size of the cueing effect in DF does not differ from that shown by controls. For further details of Crawford and Garthwaite's approach to comparing single case studies to small control samples, see http://www.abdn.ac.uk/~psy086/dept/SingleCaseMethodology.htm.

also adamant that she was entirely guessing during the perception procedure. Given that the perception procedure was completed immediately after the attention procedure, and given that DF was asked to spot the letter "T" which had been used as a prime for the previous hour and a half of testing, it is quite possible that her above-chance (66% correct) response rate reflected the fact that her own orienting response was biasing her judgements, rather than that she was perceptually discriminating the two letters.

In the attention procedure, the four control participants also showed a similar trend in their accuracy data (valid 94%, invalid 89.7%) to that seen in their reaction times, a trend that was also apparent in DF (valid 90.6%, invalid 88.8%). Although this trend was not significant in the control sample ($p = .13$), the trend shown by DF does not differ from that shown by the control sample ($p = .28$). These trends towards a priming effect on accuracy as well as RTs indicate that the RT results indicated genuine priming, and not merely a speed–accuracy tradeoff.

## Discussion

Despite a profound disruption to DF's ability to see the letter shape primes as a result of the damage to shape processing areas in her ventral stream, she showed a normal cue-contingent priming effect based on these letter shapes. This finding is clearly consistent with the hypothesis that the priming effect is mediated by the dorsal rather than the ventral stream, a matter that will be discussed further in the General Discussion.

We have previously explored DF's sensitivity to different attentional effects (de-Wit, Kentridge, & Milner, 2009) in which we found that DF was sensitive to basic spatial cueing effects (Posner, 1980) but not object-based attention effects (Scholl, 2001). The current results extend these findings by demonstrating that DF's spatial attention can be guided by shape based cue–target contingencies. We argued on the basis of our previous results with DF (and other neuroimaging research by Martinez et al., 2006) that the object representations required to guide object-based attention effects (Scholl, 2001) are developed within the ventral stream. The use of shape cues in the current experiment, however, should not lead one to confuse the effect observed here with an object-based attention effect, in which attention is preferentially allocated within a selected object. Instead this cueing effect reflects an allocation of spatial attention based on a shape–target contingency, rather than a preferential allocation of attention within a particular object. In other words, the surviving shape processing mechanisms in DF's dorsal stream are sufficient to guide her attention in response to shape cueing, but not sufficient to provide the representations necessary to enable object-based attention effects to be seen.

# GENERAL DISCUSSION

The results from both experiments are consistent with predictions based on our hypothesis that the priming seen in our peripheral shape–cue contingent paradigm derives from computations performed in the dorsal visual stream.

In everyday experience the processes of shifting attention in response to a peripheral object and consciously perceiving that object are so intimately entwined that it is difficult to "see" the distinction (see Posner, 1980, for discussion). The tasks described here provide a way of dissociating these processes in order to examine their distinct neurocognitive bases. Experiment 1 has provided evidence that when a peripheral object influenced visual attention, without necessarily entering conscious awareness, rapid activation of the dorsal visual stream was observed. Source localization identified the superior parietal lobule (SPL) as the principal source of this activation. This region shows good correspondence with earlier PET (Corbetta, Miezin, Shulman, & Petersen, 1993) and fMRI (Gitelman et al., 1999; Szczepanski,

Konen, & Kastner, 2010) studies which have suggested that superior parietal cortex plays an important role in the control of spatial attention. Vandenberghe and Gillebert (2009) review a variety of fMRI studies, and conclude that the SPL is implicated as playing a specific role in spatial shifts of attention. Moreover, in a recent fMRI study of spatial cueing, Szczepanski et al. (2010) identified a particular region in the right, but not left, SPL that carried spatial attention-related activations. This result is consistent with the lateralization observed in our sLORETA analysis. As Figure 4a and 5a show, this analysis indicated that the right superior parietal lobule was more active in the attention procedure compared to the perception procedure. Furthermore, it is exactly these dorsal stream resources that remain preserved in Patient DF, for whom a normal attentional cueing effect was revealed in Experiment 2.

In contrast, when a peripheral object required a conscious perceptual response, rapid activation of the ventral visual stream was observed in our healthy subjects. Source analysis with sLORETA indicated that the fusiform gyrus of the left hemisphere showed stronger early activation in the perception procedure relative to the attention procedure. This fusiform region is adjacent to the damaged region in DF's brain (Area LO) which has caused her inability to distinguish simple shapes. It may therefore be that the activations seen during the perceptual task in our healthy subjects arise in and around this same Area LO. Thus, the sites identified by sLORETA, when comparing activations in the attention and perception procedure*s*, correspond well with those identified in earlier research on the neural correlates of spatial attention and perceptual identification of simple shape stimuli respectively. In full agreement with this, we found in Experiment 2 that Patient DF's bilateral lesion to shape processing areas within the ventral stream led to a serious disruption to performance in the perception procedure, whereas her functionally intact dorsal stream supported entirely spared performance in the attention task.

The electrophysiological and neurological dissociations reported here are consistent with the behavioural dissociation described in our earlier study (Lambert & Shin, 2010), in which reducing luminance contrast massively impaired conscious perception of peripheral letters, but had no effect on rapid orienting in response to the same stimuli, when they acted as cues in the attention procedure. Indeed, six lines of converging evidence can now be marshalled in support of the dorsal stream attention hypothesis: (1) As we have noted, the attentional effects of peripheral letter cues are robust under low contrast, consistent with the physiological properties of the M-cell inputs to the dorsal visual pathway (Lambert & Shin, 2010). (2) Experiment 1 provided evidence of rapid dorsal activation, when bilateral letters served as spatial attentional cues. (3) Experiment 2 showed that Patient DF, in whom the ventral stream is damaged while the dorsal stream remains intact, is able

to orient in response to bilateral letter cues in the attention procedure, but performs very poorly when asked to discriminate these stimuli in the perception procedure. (4) Consistent with temporal properties of dorsal visual processing (Bullier, 2001; Milner & Goodale, 2006), peripheral letter cues affect target processing, even when cue and target stimuli are presented with brief SOAs or simultaneously (Experiment 1, zero SOA condition; Lambert & Duddy, 2002). (5) Consistent with evidence that dorsal visual processing is largely unconscious (Milner & Goodale, 2006), Lambert, Naikar, McLachlan, and Aitken (1999) and Shin et al. (2011) found that peripheral cue stimuli, including letter cues of the kind used in the current study, can influence attention independently of conscious awareness (see also Peterson & Gibson, 2011; Risko & Stolz, 2010). (6) Lambert and Duddy (2002) compared effects of bilateral letter cues presented centrally (immediately to left and right of a central cross) and 7.3° from fixation. The time course and magnitude of visual orienting effects were unaffected by whether the letter cues were presented centrally or peripherally. Although participants did not perform a perceptual control task, one would certainly expect that conscious discrimination of letters at 7.3° eccentricity would be impaired relative to discrimination of the same letters in central vision. The observation that visual orienting in response to letters is unaffected by whether they are presented centrally or at 7.3° eccentricity is consistent with the dorsal stream attention hypothesis because anatomical studies have shown that representation of peripheral visual locations is stronger in the dorsal than the ventral stream (Merigan & Maunsell, 1993). Taken together, these six empirical findings provide substantial and converging support for the hypothesis that visual encoding which triggers a shift of attention arises from processing in the dorsal visual stream.

In both the attention and perception procedures, rapid, high level activation—at superior parietal and inferior occipitotemporal sites, respectively—was followed by strong activation at "earlier" sites in the visual pathway, in occipital cortex. In contrast to the anatomical separation apparent in the early activations, the location of later activations, associated with the peak of the P1 evoked by the letter stimuli, was closely similar in the attention and perception procedures (see Figure 4c,d). The fine-grained timing of this pattern is consistent with the hypothesis that visual processing in each task involved a rapid, initial burst of feedforward activity, followed by reentrant feedback which modulated "lower level" visual computations performed in occipital cortex (Martinez et al., 1999). This proposal is consistent with previous evidence that attentional enhancement can arise from temporally late top-down modulation of activity at anatomically early sites in the visual pathway (see Olson, Chun, & Allison, 2001).

This view of perception and attention implies a startling temporal paradox, in which high level processing in either visual pathway can precede and influence ostensibly "lower" level processing. This raises the question of how high level processing can be completed with sufficient speed to affect processing at an "earlier" stage. According to Bullier's (2001) "integrated model of visual processing", rapid first-pass computations performed in the dorsal stream are followed by reentrant feedback which modulates processing in the "earlier" areas V1 and V2. According to this model, visual areas V1 and V2 can be viewed as "active blackboards", which integrate sensory, feedforward signals with reentrant, feedback signals. This "active blackboard" interpretation is consistent with a host of fMRI results highlighting that higher level perceptual interpretations are evident in the signals recorded from early areas (Harrison & Tong, 2009; Murray, Boyaci, & Kersten, 2006; Williams et al., 2008). Bullier's (2001) model therefore suggests a promising hypothesis for resolving one aspect of the seeming temporal paradox in our data. According to this hypothesis, the initial burst of feedforward processing elicited by letters when they act as spatial cues is carried by rapid onset M-system neurons in the dorsal visual pathway. Reentrant feedback from "fast brain" computations in the parietal lobe are then fed back to occipital areas in time to affect target processing within the ventral system, which leads eventually to a conscious perceptual response to the target object.

Although, as we have already noted, the temporal scenario implied by our findings appears surprising and paradoxical, it is nevertheless consistent with data gained from electrophysiological studies, regarding the speed of visual processing (see Tovee, 1994). It is important to remember here that for the letter cues to be effective in the attention procedure, it is not necessary to process them *as letters*. The cues are drawn from a stimulus set comprising just two items ("X" or "T"), and these stimuli differ at a very basic perceptual level: The former comprises two oblique lines, whereas the latter comprises one vertical and one horizontal line. It is known that simple attributes, such as line orientation are extracted early in visual processing, at V1. Three observations are pertinent here. First, Tovee (1994) notes that cells with transient responses, which provide the major input for the dorsal stream, respond with an average latency of 28 ms. Second, by recording from successive areas in the visual processing stream, it has been estimated that it takes about 10–15 ms for signals to be transmitted from one area (e.g., V1) to a succeeding area (e.g., V2; see Tovee, 1994). Third, by recording from a large number of cells simultaneously, it is possible to estimate how long it takes for the visual signal associated with one stimulus to be discriminated from the visual signal associated with another stimulus. Although the very simple stimulus discrimination ("X" vs. "T") used in this study has not, to

our knowledge, been examined in this fashion, more complex stimuli, including faces, have been studied in this way. In reviewing this work, Tovee suggests that most of the information encoded in a spike train is available 20–50 ms from the onset of that spike train (see also Rolls & Tovee, 1994; Tovee & Rolls, 1995). Our interpretation of Experiment 1 implies that cue discrimination can be achieved very rapidly, within 80–110 ms from stimulus onset. Though rapid, this temporal scenario is entirely consistent with data gained from electrophysiological studies, which have examined the time course of visual processing directly, using single cell and multiple cell recording techniques.

Our prediction that the perception procedure would generate stronger ventral activation than the attention procedure was confirmed, but our prediction that this activation would follow a slower time course than that associated with dorsal (attention procedure) activation was disconfirmed. It is noteworthy that dorsal–ventral differentiation between evoked activity in the two task contexts involved not only early dorsal activation in the attention procedure, as predicted, but also early ventral activation in the perception procedure. We predicted that the latter would have a somewhat slower time course than the dorsal "fast brain" activation associated with the attention procedure (Bullier, 2001). As noted earlier, peripheral letters presented in the context of the perception procedure, served as perceptual previews—participants released a conscious perceptual response to the letters, when they were presented again, 700 ms after onset of the preview display. This design feature ensured that the two tasks shared an identical temporal structure, but it also meant that the preview display acted as an identity cue, which predicted the nature and location of the letters on the succeeding display with perfect fidelity. One possible interpretation of early ventral activation in the perception procedure (see Figure 4b) is to propose that while encoding of spatial primes is mediated, as we have shown, by rapid dorsal activation, encoding of identity primes is mediated via rapid ventral activation, perhaps mediated by the rapidly conducting M component of the ventral stream. Further neuroimaging studies which compare directly the neural correlates of spatial and identity priming will be required to test these hypotheses.

Although our interpretation of the performance in the perception procedure has emphasized that participants make a direct conscious response to the letters, it is also germane to note that the incorporation of a delay in the perception procedure means that it can also be characterized as a working memory task. To the extent that one identifies working memory representations with representations that are maintained in conscious awareness, the perception procedure can be described as a working memory task. However, it is worth remembering that in both the attention procedure

and the perception procedure participants make a directional response that is determined by the nature of the peripheral cue items.

Our results with Patient DF suggest strongly that visual letter shapes can be coded within the dorsal stream independently of the ventral stream. Our data suggest further that this coded information can impact directly upon attentional structures within the dorsal stream, the most prominent of which is the lateral intraparietal (LIP) complex. There is in fact good evidence not only for shape coding within dorsal stream areas dedicated for guiding hand and other bodily movements (James et al., 2003), but also within the LIP itself (Janssen, Srivastava, Ombelet, & Orban, 2008; Lehky & Sereno, 2007; Sereno & Amador, 2006). It has been proposed that this kind of coding within the LIP complex may be useful in everyday life in constructing salience maps of complex visual scenes for the guidance of attention within those scenes (Arcizet, Mirpour, & Bisley, 2011). Thus, our results may also have implications for understanding the neurocognitive processes that are recruited in visual search tasks, and in particular with regard to the role of interactions between dorsal and ventral stream processing during visual search (see Vidyasagar, 1999).



## SUMMARY AND CONCLUSIONS

Both the ventral and dorsal streams were responsive to peripheral shapes, consistent with the idea that "object" or "what" processing is a feature of both streams. However, the response to these shapes in each stream was selective for the task performed by the participant. We found that areas in the ventral stream were primarily responsive to the perceptual discrimination of our letter shapes, and indeed the ventral stream lesion in Patient DF was associated with a profound disruption of the recognition of those shapes. In contrast, areas in the dorsal stream were primarily responsive to the use of these letter shapes as attentional cues, and indeed the preservation of these dorsal areas in Patient DF was associated with a normal shape contingent cueing effect. These results are consistent with Milner and Goodale's (1995, 2006) contention that shape information is used by both streams, but for very different purposes.

The introduction outlined an apparent paradox between the ventral stream's role in conscious shape perception, and the profound influence that dorsal stream lesions have on conscious perception in extinction and neglect. The current results might help to resolve this paradox by demonstrating that the dorsal stream is able to rapidly compute perceptual contingencies that can be used to guide processing resources via a rapid feedback to occipital areas, thus highlighting how the unconscious learning of shape cue contingencies and the allocation of processing resources on the basis of

those contingencies can have a clear influence on conscious perception. These results therefore highlight not only an important functional specialization between the two streams in their role in perception and attention, but also how these two streams might interact to ensure that the focus of action and the focus of perception is unified via the allocation of attention.



## REFERENCES


Anllo-Vento, L. (1995). Shifting attention in visual space: The effects of peripheral cueing on brain cortical potentials. *International Journal of Neuroscience*, *80*(1–4), 353–370.

Anllo-Vento, L., Schoenfeld, M. A., & Hillyard, S. A. (2004). Cortical mechanisms of visual attention. In M. I. Posner (Ed.), *Cognitive neuroscience of attention* (pp. 180–193). New York, NY: Guilford Press.

Arcizet, F., Mirpour, K., & Bisley, J. W. (2011). A pure salience response in posterior parietal cortex. *Cerebral Cortex*, *21*(11), 2498–2506.

Bullier, J. (2001). Integrated model of visual processing. *Brain Research Reviews*, *36*, 96–107.

Corbetta, M., Miezin, F. M., Shulman, G. L., & Petersen, S. E. (1993). A PET study of visuospatial attention. *Journal of Neuroscience*, *13*, 1202–1226.

Crawford, J. R., & Garthwaite, P. H. (2002). Investigation of the single case in neuropsychology: Confidence limits on the abnormality and test score differences. *Neuropsychologia*, *40*, 1196–1208.

Crawford, J. R., & Garthwaite, P. H. (2007). Comparison of a single case to a control or normative sample in neuropsychology: Development of a Bayesian approach. *Cognitive Neuropsychology*, *24*, 343–372.

de-Wit, L. H., Kentridge, R. W., & Milner, A. D. (2009). Object-based attention and visual area LO. *Neuropsychologia*, *47*(6), 1483–1490.

Doallo, S., Lorenzo-Lopez, L., Vizoso, C., Rodriguez Holguin, S., Amenedo, E., Bara, S., et al. (2004). The time course of the effects of central and peripheral cues on visual processing: An event-related potentials study. *Clinical Neurophysiology*, *115*(1), 199–210.

Eimer, M. (1996). The N2pc component as an indicator of attentional selectivity. *Electroencephalography and Clinical Neurophysiology*, *99*, 225–234.

Fang, F., & He, S. (2005). Cortical responses to invisible objects in the human dorsal and ventral pathways. *Nature Neuroscience*, *8*(10), 1380–1385.

Fuchs, M., Kastner, J., Wagner, M., Hawes, S., & Ebersole, J. S. (2002). A standardized boundary element method volume conductor model. *Clinical Neurophysiology*, *113*, 702–712.

Gitelman, D. R., Nobre, A., Parrish, T. B., LaBar, K. S., Kim, Y.-H., Meyer, J. R., et al. (1999). A large-scale distributed network for covert spatial attention: Further anatomical delineation based on stringent behavioural and cognitive controls. *Brain*, *122*, 1093–1106.

Harrison, S. A., & Tong, F. (2009). Decoding reveals the contents of visual working memory in early visual areas. *Nature*, *458*(7238), 632–635.

Harter, M. R., Miller, S. L., Price, N. J., LaLonde, M. E., & Keyes, A. L. (1989). Neural processes involved in directing attention. *Journal of Cognitive Neuroscience*, *1*, 223–237.

He, X., Humphreys, G., Fan, S., Chen, L., & Han, S. (2008). Differentiating spatial and object-based effects on attention: An event-related brain potential study with peripheral cueing. *Brain Research*, *1245*, 116–125.

Hopfinger, J., & Mangun, G. R. (2001). Tracking the influence of reflexive attention on sensory and cognitive processing. *Cognitive, Affective, and Behavioral Neuroscience*, *1*, 56–65.

James, T. W., Culham, J., Humphrey, G. K., Milner, A. D., & Goodale, M. A. (2003). Ventral occipital lesions impair object recognition but not object-directed grasping: a fMRI study. *Brain*, *126*, 2463–2475.

Janssen, P., Srivastava, S., Ombelet, S., & Orban, G. A. (2008). Coding of shape and position in macaque lateral intraparietal area. *The Journal of Neuroscience*, *28*(26), 6679–6690.

Jongen, E. M., Smulders, F. T., & van der Heiden, J. S. (2007). Lateralized ERP components related to spatial orienting: Discriminating the direction of attention from processing sensory aspects of the cue. *Psychophysiology*, *44*, 968–986.

Jurcak, V., Tsuzuki, D., & Dan, I. (2007). 10/20, 10/10, and 10/5 systems revisited: Their validity as relative head-surface-based positioning systems. *NeuroImage*, *34*, 1600–1611.

Kentridge, R. W., Heywood, C. A., & Weiskrantz, L. (1999). Attention without awareness in blindsight. *Proceedings of the Royal Society: Biological Sciences*, *266B*(1430), 1805–1811.

Kiss, M., van Velzen, J., & Eimer, M. (2008). The N2pc component and its links to attention shifts and spatially selective processing. *Psychophysiology*, *45*, 240–249.

Klein, R. (2004). On the control of visual orienting. In M. I. Posner (Ed.), *Cognitive neuroscience of attention* (pp. 29–44). New York, NY: Guilford Press.

Lambert, A. J. (2003). Visual orienting, learning and conscious awareness. In L. Jimenez (Ed.), *Attention and implicit learning* (Vol. 48, pp. 253–276). Amsterdam, The Netherlands: John Benjamins.

Lambert, A. J., & Duddy, M. (2002). Visual orienting with central and peripheral precues: Deconfounding the contributions of cue eccentricity, cue discrimination and spatial correspondence. *Visual Cognition*, *9*(3), 303–336.

Lambert, A. J., & Hockey, G. R. J. (1986). Selective attention and performance with a multi-dimensional visual display. *Journal of Experimental Psychology: Human Perception and Performance*, *12*, 484–495.

Lambert, A. J., & Holmes, J. (2004). Ageing and visual orienting in response to complex spatial cues. *Brain Impairment*, *5*, 1–9.

Lambert, A. J., Naikar, N., McLachlan, K., & Aitken, V. (1999). A new component of visual orienting: Implicit effects of peripheral information and sub-threshold cues on covert attention. *Journal of Experimental Psychology: Human Perception and Performance*, *25*, 321–340.

Lambert, A. J., Norris, A., Naikar, N., & Aitken, V. (2000). Effects of informative peripheral cues on eye movements: Revisiting William James "derived attention". *Visual Cognition*, *7*, 545–569.

Lambert, A. J., Roser, M., Wells, I., & Heffer, C. (2006). The spatial correspondence hypothesis and orienting in response to central and peripheral precues. *Visual Cognition*, *13*, 65–88.

Lambert, A. J., & Shin, M.-J. (2010). The hare and the snail: Dissociating visual orienting from conscious perception. *Visual Cognition*, *18*(6), 829–838.

Lehky, S. R., & Sereno, A. B. (2007). Comparison of shape encoding in primate dorsal and ventral visual pathways. *Journal of Neurophysiology*, *97*(1), 307–319.

Luck, A. J., & Hillyard, S. A. (1994). Spatial filtering during visual search: Evidence from human electrophysiology. *Journal of Experimental Psychology: Human Perception and Performance*, *20*, 1000–1014.

Malach, R., Reppas, J. B., Benson, R. B., Kwong, K. K., Jiang, H., Kennedy, W. A., et al. (1995). Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. *Proceedings of the National Academy of Sciences USA*, *92*, 8135–8138.

Manly, B. F. J. (2007). *Randomization, bootstrap and Monte Carlo methods in biology* (3rd ed.). Boca Raton, CA: Chapman & Hall.

Martinez, A., Anllo-Vento, L., Sereno, M., Frank, L., Buxton, R., Dubowitz, D., et al. (1999). Involvement of striate and extrastriate visual cortical areas in spatial attention. *Nature Neuroscience*, *2*, 364–369.

McDonald, J. J., & Green, J. J. (2008). Isolating event-related potential components associated with voluntary control of visuo-spatial attention. *Brain Research*, *1227*, 96–109.

Merigan, W. H., & Maunsell, J. H. R. (1993). How parallel are the primate visual pathways? *Annual Review of Neuroscience*, *16*, 369–402.

Milner, A. D., & Goodale, M. A. (1995). *The visual brain in action* (1st ed.). Oxford, UK: Oxford University Press.

Milner, A. D., & Goodale, M. A. (2006). *The visual brain in action* (2nd ed). Oxford, UK: Oxford University Press.

Milner, A. D., Perrett, D. I., Johnstone, R. S., Benson, P. J., Jordan, T. R., Heeley, D. W., et al. (1991). Perception and action in "visual form agnosia". *Brain*, *114*, 405–428.

Mishkin, M., Ungerleider, L., & Macko, S. (1983). Object vision and spatial vision: Two cortical pathways. *Trends in Neurosciences*, *6*, 414–417.

Murray, S. O., Boyaci, H., & Kersten, D. (2006). The representation of perceived angular size in human primary visual cortex. *Nature Neuroscience*, *9*(3), 429–434.

Nichols, T. E., & Holmes, A. P. (2001). Nonparametric permutation tests for functional neuroimaging: A primer with examples. *Human Brain Mapping*, *15*, 1–25.

Niemi, P., & Naataanen, R. (1981). Foreperiod and simple reaction time. *Psychological Bulletin*, *89*, 133–162.

Nobre, A. C., Sebestyen, G. N., & Miniussi, C. (2000). The dynamics of shifting visuospatial attention revealed by event related potentials. *Neuropsychologia*, *38*, 964–974.

Olson, I., Chun, M., & Allison, T. (2001). Contextual guidance of attention: Human intracranial event related potential evidence for feedback modulation in anatomically early, temporally late stages of visual processing. *Brain*, *124*, 1417–1425.

Pascual-Marqui, R. D. (2002). Standardized low-resolution brain electromagnetic tomography (sLORETA): Technical details. *Methods and Findings in Clinical and Experimental Pharmacology*, *24D*, 5–12.

Peterson, S. A., & Gibson, T. N. (2011). Implicit orienting in a target detection task with central cues. *Consciousness and Cognition*, *20*(4), 1532–1547.

Posner, M. I. (1980). Orienting of attention. *Quarterly Journal of Experimental Psychology*, *32*, 3–25.

Praamstra, P., & Kourtis, D. (2010). An early parietal ERP component of the frontoparietal system: EDAN does not equal N2pc. *Brain Research*, *1317*, 203–210.

Risko, E. F., & Stolz, J. A. (2010). The proportion valid effect in covert orienting: Strategic control or implicit learning? *Consciousness and Cognition*, *19*, 432–442.

Rolls, E. T., & Tovee, M. J. (1994). Processing speed in the cerebral cortex and the neurophysiology of backward masking. *Proceedings of the Royal Society of London: Biological Sciences*, *257*, 9–15.

Scholl, B. (2011). Objects and attention: The state of the art. *Cognition*, *80*(1–2), 1–46.

Sereno, A. B., & Amador, S. C. (2006). Attention and memory-related responses of neurons in the lateral intraparietal area during spatial and shape-delayed match-to-sample tasks. *Journal of Neurophysiology*, *95*(2), 1078–1098.

Shin, M.-J., Marrett, N., & Lambert, A. J. (2011). Visual orienting in response to attentional cues: Spatial correspondence is critical, conscious awareness is not. *Visual Cognition*, *19*, 730–761.

Szczepanski, S. M., Konen, C. S., & Kastner, S. (2010). Mechanisms of spatial attention control in frontal and parietal cortex. *Journal of Neuroscience*, *30*, 148–160.

Tovee, M. J. (1994). How fast is the speed of thought? *Current Biology*, *4*, 1125–1127.

Tovee, M. J., & Rolls, E. T. (1995). Information encoding in short firing rate epochs by single neurons in primate temporal cortex. *Visual Cognition*, *1*, 35–58.

Vandenberghe, R., & Gillebert, C. R. (2009). Parcellation of parietal cortex: Convergence between lesion-symptom mapping and mapping of the intact functioning brain. *Behavioural Brain Research*, *199*, 171–182.

Van Velzen, J., & Eimer, M. (2003). Early posterior ERP components do not reflect the control of attentional shifts toward expected peripheral events. *Psychophysiology*, *40*, 827–831.

Vidyasagar, T. R. (1999). A neuronal model of attentional spotlight: Parietal guiding the temporal. *Brain Research Reviews*, *30*, 66–76.

Williams, M., Baker, C., Op de Beeck, H., Shim, W., Dang, S., Triantafyllou, C., & Kanwisher, N. (2008). Feedback of visual object information to foveal retinotopic cortex. *Nature Neuroscience*, *11*(12), 1439–1445.

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